

The Role of Endangered Species Reintroduction in Ecosystem Restoration: Tortoise–Cactus Interactions on Española Island, Galápagos

James P. Gibbs,^{1,2} Cruz Marquez,³ and Eleanor J. Sterling⁴

Abstract

We evaluated the role that endangered species reintroduction efforts can play in the larger context of ecosystem restoration. To do so, we examined interactions between endangered giant tortoises (*Geochelone nigra hoodensis*), currently being reintroduced to Isla Española, Galápagos, and an arboreal cactus (*Opuntia megasperma* var. *megasperma*), which is itself endangered and a keystone resource for many animals on the island. We collected information on spatial patterns of occurrence of cacti, tortoises, and woody vegetation and compared recruitment of juvenile cacti in areas occupied versus unoccupied by tortoises. Reintroduced tortoises appeared to suppress cactus recruitment near the few remaining adult cacti at the study site, but facilitate it at

longer distances, with tortoise–cactus interactions mediated by the presence of woody vegetation, which likely alters tortoise movements and thereby patterns of cactus seed dispersal. The net effect of tortoises on cacti appeared to be positive insofar as tortoise presence was associated with greater recruitment of juveniles into cactus populations. Our study provides support for reintroducing endangered reptiles and other animals to aid ecosystem restoration in areas where they might once have played an important role in grazing upon and dispersing plants.

Key words: cactus, endangered species, Galápagos Islands, *Geochelone*, *Opuntia*, reintroduction, restoration ecology, tortoise.

Introduction

Species reintroduction typically involves establishment from translocated stock of a new population of a threatened or endangered species after harmful conditions in the original habitat have been corrected. Reintroduction is a key component of integrated strategies for recovery of many endangered species (Griffith et al. 1989; Dodd & Siegel 1991; Falk & Olwell 1992). In general, reintroduction studies focus on the autecology of the species being reintroduced, particularly when they are endangered species (see Sarrazin & Barbault 1996). However, endangered species reintroduction can also reinstate key ecological processes, particularly where important mutualisms have been disrupted (Bond 1994). One recent example involves wolves in Yellowstone National Park in the western United States, where the reintroduced animals have altered herbivore feeding patterns and thereby changed patterns of woody plant regeneration and avian diversity over large areas (Ripple & Beschta 2004). Simi-

larly, a reintroduced population of European beavers in France rejuvenated riparian forests and helped stabilize riverbanks (Fustec et al. 2001). Unfortunately, a lack of comparable assessments for other endangered taxa and other regions hinders our understanding of whether endangered species reintroduction efforts can play a significant role in the larger context of ecosystem restoration or whether their primary purpose is recovery of lost amenity value associated with species extinction (e.g., Langford et al. 2001). Similarly, little information is available regarding the time it takes for systems to adapt to the reintroductions, although evidence from wolf reintroductions in North America point to rapid (within one generation) development of predator–prey relationships (Berger et al. 2001).

We conducted a preliminary assessment of the ecological consequences of a species reintroduction program on Española Island in the Galápagos Archipelago—the site of one of the most successful and ambitious yet least heralded species reintroduction efforts. Our focus was giant tortoises (*Geochelone nigra hoodensis*), which once numbered perhaps 3,000 on the island, but by 1965, had been reduced to just 14 individuals primarily by hunters from sealing, whaling, and pirate ships (Pritchard 1996). As an emergency conservation measure in the mid-1960s, remaining tortoises were transferred to the Breeding Center of the Charles Darwin Research Station and Galápagos National Park on Isla Santa Cruz. During the 1970s, about 3,000 goats were eliminated from Española as the result of an intense campaign by guards of the Galápagos National

¹ State University of New York, College of Environmental Science and Forestry, Syracuse, NY 13210, U.S.A.

² Address correspondence to J. P. Gibbs, email jpgibbs@esf.edu

³ Charles Darwin Research Station, Puerto Ayora, Santa Cruz, Galápagos Islands, Ecuador

⁴ Center for Biodiversity and Conservation, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024, U.S.A.

Park Service, and thus, the recovery of the vegetation, which goats had devastated for at least a century, probably began as early as mid-1970s. Since 1971, the captive tortoise population has generated more than 1,200 offspring, all of which have been repatriated to Española. Repatriated tortoises are now reproducing in situ and may have regained about one-third of their original density (J. P. Gibbs, SUNY-ESF, personal observation, 2007).

The vegetation has also recovered on Española because the elimination of wild goats, with the notable exception of an unusual, large-seeded, and arboreal cactus (*Opuntia megasperma* var. *megasperma*) whose populations were affected by goats, which prevented recruitment and toppled adult cacti (Coronel 2002). The cactus' global range is restricted to just three islands in the archipelago. The cactus is currently regarded as "endangered" on Española by the World Conservation Union because subpopulations on one part of the island have entirely disappeared and the rate of regeneration throughout the island is, for reasons that are unclear, extremely low even after the removal of goats (Grant & Grant 1989; Marquez et al. 2003). Because the tortoises depend on the cactus for shade, food, and moisture during the drier parts of the year, the lack of cacti may affect the long-term viability of the reintroduced tortoise population. Moreover, the cactus is a keystone resource for most other terrestrial vertebrate animals on the island, providing food, moisture, and shade throughout the drier parts of the year (Hicks & Mauchamp 1996).

One plausible explanation for the cactus' status is that recruitment processes have resumed only recently with the reappearance of tortoises repatriated to the island. Although Galápagos cacti reproduce by a variety of sexual and asexual modes, dispersal of seeds by animals is important (Hicks & Mauchamp 2000). Tortoises are known to be important seed dispersers elsewhere (e.g., Hnatiuk 1978; Carlson et al. 2003), and the cactus may well depend on the tortoises for seed germination and dispersal. Germination rates for the native Galápagos tomato are higher if seeds are passed through the digestive tracts of tortoises (Rick & Bowman 1961), and the same may apply to Galápagos cacti (Estupinian & Mauchamp 1995; Dawson 1966). Another possible factor is rapid expansion of woody vegetation on the island in the absence of both goats and tortoises. Tortoises at typical densities maintain open areas through browsing and mechanical damage from their shells (Hamann 2001), but in their absence, woody vegetation can expand and out-compete young cacti for light (Hicks & Mauchamp 2000). A further consideration is that remaining cacti may have become too sparsely distributed on the island as a result of goat depredations to effectively crosspollinate one another (an "Allee effect," e.g., Forsyth [2003], although the occurrence of apomixis in some *Opuntia* [Mondragon-Jacobo & Pimienta-Barrios 1995] may render such effects obsolete).

Because of the conservation significance of both the cactus and the tortoise, the potential interaction between

them, and the keystone role that the cacti play in the island's terrestrial ecology, we evaluated through a field study in 2004 the spatial patterns of occurrence of cacti, tortoises, and woody vegetation. We also compared cactus population structure in areas occupied versus unoccupied by tortoises on the island and examined temporal trends in cactus population structure at a site occupied by reintroduced tortoises. These comparisons permitted us to evaluate the hypothesis that the reintroduction of the endangered tortoises facilitates recovery of the cactus and thus plays a larger role in restoration of the island's terrestrial ecosystem.

Methods

The spatial distribution of cactus and tortoises was surveyed during the dry season between 23 March and 4 April 2004 in a contiguous, 60 ha area in the region known as "Las Tunas." The area is dominated by loose rock, herbaceous cover (mainly *Galactea striata* and *G. tenuiflora*, and *Phaseolus mollis* and *Rhynchosia minima*) and patches of woody vegetation (mainly *Cordia lutea* and *Prosopis juliflora*) interspersed with cacti (Fig. 1). The area surveyed encompassed one of the two primary release sites for tortoises repatriated on Española to date. The area was gridded into 25 × 25 m survey blocks, and each was searched to locate all cacti, including juveniles (trunk entirely spiny), subadults (trunks with both spines and bark), and adults (trunk entirely bark covered). Location of each cactus was recorded with a handheld global positioning system unit (Garmin III+) accurate to about



Figure 1. The Las Tunas study area on Española Island in the Galápagos Archipelago where tortoise–cactus interactions were studied March to April 2004. A tortoise (with straight-line length of the lower portion of the shell of about 60 cm) rests to the left of the cactus' trunk. Note the dearth of any young cacti at the base of this fruiting adult cactus. Woody vegetation is evident in the background (Photo by J. P. Gibbs).

2 m. We recorded for all cacti maximum height (m) as well as percent woody cover and number of intact tortoise droppings within a 2.5-m radius circle surrounding the cactus stem. The cigar-shaped and -sized tortoise droppings are highly conspicuous and persist for about 1 year in this arid environment and thus serve as a useful indicator of cumulative patterns of tortoise occurrence. For juvenile cacti, we also recorded the number of cladodes present. For adult cacti, we recorded the number of fruits present. Woody cover and number of tortoise droppings within a 2.5-m radius circle were also estimated at 96 points located randomly within the study area boundary.

Positional data for all cacti and tortoises were input into a geographic information system (ArcView 3.2, Redlands, CA, U.S.A.) to determine the distance of all tortoise droppings and cacti to the nearest adult cactus. To avoid “edge effects” imposed by the study area boundary, any individual adult cactus situated closer to a study area boundary than to another adult cactus was used as a potential neighbor in any nearest neighbor analyses performed but was not used as a datum. To examine interactions among the distribution of woody cover, tortoises, and cacti, we used a one-way analysis of variance to contrast estimated percent woody cover among cacti of the three stages and random points where tortoise droppings were and were not present; Tukey’s honestly significant difference post hoc multiple range test was used to identify which, if any, of these five class means were different. To examine whether individual isolation may have limited cactus reproduction, number of fruits counted on an adult cactus was regressed against both cactus height and nearest neighbor distance. All distance data were \log_{10} transformed for normality, and proportion data were transformed as $\arcsin\sqrt{p}$ for analysis.

Comparison of our data to that of other studies of cacti on the island permitted further insights. In the late 1990s, Coronel (2002) surveyed cactus populations elsewhere on the island at sites where the tortoises do not occur, thus permitting us to compare size structure in cactus populations in relation to the presence of tortoises. Furthermore, Marquez et al. (2003) collected data at our study site 10 years previously, enabling us to examine temporal trends in the cactus population at a site long occupied by tortoises. For both comparisons, frequency distributions of stage classes of cacti were compared using a G test for a contingency table (Sokal & Rohlf 1995).

Results

Spatial Variation in Cactus Stage Distributions Across the Island

We located 125 adult cacti (39% of cacti, 2.12/ha), 34 subadult cacti (11%, 0.58/ha), and 160 juvenile cacti (50%, 2.72/ha) in the Las Tunas study area. At sites where tortoises do not occur on Española Island, as reported by Coronel (2003, i.e., sites other than Las Tunas, “El Caco,” and “Cerro Rojo”), stage distributions were 60% adults,

10% subadults, and 30% juveniles ($n = 106$ cacti). These distributions differ significantly ($df = 2$, $G_{\text{adjusted}} = 15.8$, $p < 0.001$), indicating that presence of tortoises was associated with a higher relative representation of juveniles in local cactus populations.

Temporal Variation in Cactus Density and Age Distribution of Juvenile Cacti

Marquez et al. (2003) surveyed *Opuntia* in our study area 10 years prior to our study and reported an overall density of juveniles of less than or equal to eight cladodes at 61 juveniles/km² (95% confidence intervals about mean: 32.5–89.4 juveniles/km²), with 35% of the 92 juveniles encountered being of a large size (five to eight cladodes). Ten years later, at the same site we observed juveniles of less than or equal to eight cladodes at a density of 190/km², with 80% of the 112 juveniles encountered being of a large size (four to eight cladodes), suggesting that juvenile density had increased and juveniles were considerably larger after 10 years in the presence of a reintroduced population of tortoises.

Interactions Among Cacti, Tortoises, and Woody Vegetation

Mean distances to the nearest adult cactus varied among cacti of different stages ($df = 4$, 448, $F = 31.9$, $p < 0.001$; Fig. 2). Post hoc, multiple comparison tests indicated that subadult cacti, juvenile cacti, and random points were of comparable and greater distance from adult cacti than adult cacti were from each other. Mean woody cover also varied ($df = 4$, 448, $F = 17.8$, $p < 0.001$): adult, subadult, and juvenile cacti had similar ($p > 0.05$) levels of cover, but collectively less woody cover ($p < 0.05$) than occurred at random points (Fig. 2). Mean number of tortoise droppings also varied ($df = 4$, 448, $F = 17.8$, $p < 0.001$), such that low, but comparable numbers of droppings occurred near juvenile and subadult cacti and random points, whereas higher numbers of droppings occurred near adult cacti (Fig. 2). Finally, in comparison to random points with droppings present, random points with no droppings had more woody cover (48.1 ± 5.17 vs. 24.5 ± 4.03 , $df = 94$, $t = 3.328$, $p = 0.001$) and were closer to adult cacti (53.2 ± 4.12 vs. 41.0 ± 3.81 , $df = 94$, $t = 2.07$, $p = 0.041$; Fig. 2).

Relationship Between Fruit Set and Adult Isolation

Fruit set on adult cacti was related positively and significantly to cactus height and related negatively, but not significantly, to distance to the nearest other adult cactus (Table 1).

Discussion

Although cactus populations are subject to episodic recruitment (Godinez-Alvarez et al. 2003) and hence any single-year study is vulnerable to sampling anomalies, the extensive temporal and spatial scale of our comparisons

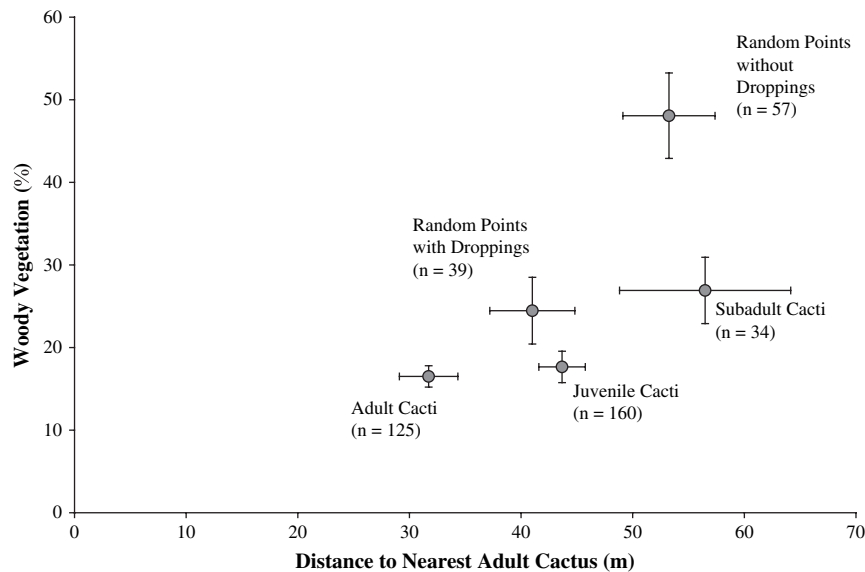


Figure 2. Spatial pattern of the occurrence of cacti and tortoises (as indicated by the locations of their droppings) in relationship to extent of woody vegetation (percent cover) and distance to nearest adult cactus ($\bar{X} \pm 95\%$ confidence intervals), March to April 2004 Las Tunas, Española Island, Galápagos.

suggest that the patterns observed may be reflective of population-wide changes in cactus on Isla Española. In general, our study suggests that cactus recovery may have been facilitated by reintroduction of tortoises. Juvenile representation in cactus populations was higher in tortoise-occupied areas relative to nonoccupied areas and also increased over time in one of the main areas of the island occupied by tortoises. The latter result is somewhat confounded, however, by the simultaneous extermination of goats from the same area, such that cactus recovery there could be a function of cessation of the trampling and browsing by goats as much as reappearance of tortoises.

The precise mechanisms by which tortoises facilitate cactus regrowth are unknown, but spatial patterns of tortoise activity, cacti, and woody cover suggest a complex set of tortoise–cactus interactions. In general, results are consistent with the hypothesis that tortoises suppress cactus regeneration near seed sources, given that fewer juvenile and subadult cacti were observed near adult cacti than were other adult cacti. This is unusual insofar as seedling recruitment is often related to distance from adult in a negative exponential manner (i.e., outside of the immediate zone of influence of the parent plant; Ribbens

et al. 1994). The reverse pattern may occur on Isla Española because substrates below adult cacti are major loci of tortoise activity; tortoises expend considerable effort seeking fallen fruits and pads or shade there and consume virtually all fruits that fall, as was indicated by the higher frequency of random points with droppings near adult cacti than random points without. Notably, higher densities of tortoise droppings should result in higher cactus seed deposition and hence higher juvenile recruitment near adult cacti, but this was not observed. Small cactus seedlings, although heavily armored (Dawson 1966), are likely susceptible to mechanical damage caused by trampling and flattening by tortoises. Lava lizards, mockingbirds, and finches also eat or damage the young cacti (Coronel 2002), but, unlike the tortoises, their activities do not show as pronounced an association with adult cacti (J. P. Gibbs, personal observations) and hence are not likely to structure cactus recruitment in relation to adult cacti to the degree that tortoises do. It is also possible that shade associated with adult plants suppresses recruitment near them, but the shade produced by the adults' cladodes tends to be highly spotty given the sparse canopy formed by adult cacti.

In contrast, patterns of deposition of tortoise droppings suggest that tortoises may facilitate cactus recruitment in areas remote from adult cacti and with little woody cover. We suggest that this occurs because tortoises focus their activities near adult cacti for much of the year, but when moving among cactus patches avoid woody cover. The tortoises have difficulty moving through woody cover because of their bulk. Moreover, edges of the carapace of the subspecies studied exhibit a characteristic and pronounced flaring as well as distinct “saddle-back”

Table 1. Relationship between number of fruits on an adult cactus ($n = 107$) versus adult cactus height and distance to nearest other adult cactus at Las Tunas, Española Island, April to May 2004.

	Estimate	SE	<i>t</i>	<i>p</i>
Constant	−0.715	0.411	−1.7	0.085
Nearest neighbor distance (m)	−0.004	0.003	−1.6	0.115
Cactus height (m)	0.284	0.091	3.1	0.002

morphology to the shell (Pritchard 1996) that tends to snag on woody stems. Although competition for light with woody vegetation is an important mechanism limiting recruitment of *Opuntia* on other islands (Hicks & Mauchamp 2000), on Isla Española tortoises evidently did not penetrate areas dominated by woody vegetation, as indicated by a lack of droppings in woody areas far from adult cacti. We therefore suggest that limitation on tortoise movement imposed by woody vegetation limits seed dispersal into woody areas and is the primary means by which woody vegetation currently affects patterns of cactus recruitment, growth, and distribution. Other vertebrates on the island (finches, mockingbirds, and lava lizards) consume cactus seeds and move freely through woody vegetation but are primarily seed predators (Hicks & Mauchamp 1996).

Small population size in rare plants can limit seed set and reduce population growth (e.g., Forsyth 2003). For *Opuntia megasperma*, we found only a weak negative relationship between fecundity and nearest neighbor distance. Breeding systems are not well known for Galápagos *Opuntia* (Hicks & Mauchamp 1996), but in other *Opuntia*, breeding may occur by apomixis or amphimixis (Mondragon-Jacobo & Pimienta-Barrios 1995), so perhaps outcrossing is not important in this species. In contrast, adult height was strongly correlated with fruit set (see also Racine & Downhower 1974 for similar relationships in other Galápagos *Opuntia* and Godinez-Alvarez et al. 2003 for cacti generally). This suggests that as more cacti mature on the island, reproductive output of the cactus population will increase. However, elsewhere on the island, where cactus populations are exceedingly reduced (Coronel 2002), pollination may be more limiting, and should be assessed.

Restoration Implications

This study has broader implications for ecosystem restoration wherever saurochory (seed dispersal by reptiles) was once important. The highest animal biomass in many arid regions often is associated with reptiles (e.g., Rodda et al. 2001), which can play an important role in regulating vegetation through grazing and by dispersing seeds. Reptiles are disproportionately threatened by human activities relative to other vertebrate animals (Gibbons et al. 2000). We have shown that reintroduced tortoises may positively affect endangered cacti that are also ecological keystones of an arid region, highlighting the importance of restoring endangered animals as part of restoration ecology efforts (e.g., Hamblen 1994). Similar conclusions have been reached in studies of large-seeded plants and endangered and extinct pigeons (Clout & Hay 1989) and fruit bats (Cox et al. 1991) on other islands of the Pacific Ocean. Additionally, this study provides empirical support for recommendations made earlier by Hamann (1993) to reintroduce tortoises to areas of Galápagos where they have disappeared to sustain floristic diversity.

Nevertheless, our study still represents a preliminary investigation into tortoise–cactus interactions on Española Island. Research to better clarify interactions might focus on: (1) studies of germination effects and gut passage time for cactus seed consumed by tortoises; (2) detailed studies of tortoise movement, for example, through thread spooling or GPS devices, to better understand movement patterns and seeds dispersal capability of tortoises; (3) manipulations of woody vegetation and fencing of areas near adult cacti perhaps in conjunction with experimental planting of cactus seedlings to examine the fates of seedlings differently exposed to tortoises and other potential vertebrate animal seed dispersers and predators, adult cacti, and competition from other plants; (4) manipulations of woody vegetation to examine interactions with tortoise movement; (5) more extensive surveys of cactus populations on various parts of the island with different degrees of exposure to reintroduced tortoises; and (6) an integrated, long-term monitoring program to simultaneously track on permanent plots temporal changes in populations of both cacti and tortoises.

Implications for Practice

- Seed dispersal by reptiles, which represent the highest animal biomass in many tropical, arid ecosystems, can be important to many plants by leading to greater dispersal distances and higher rates of seed germination.
- Endangered species reintroduction programs, especially those for turtles and lizards, may reinstate key ecological processes, particularly where important plant–reptile mutualisms have been disrupted by human activities.

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